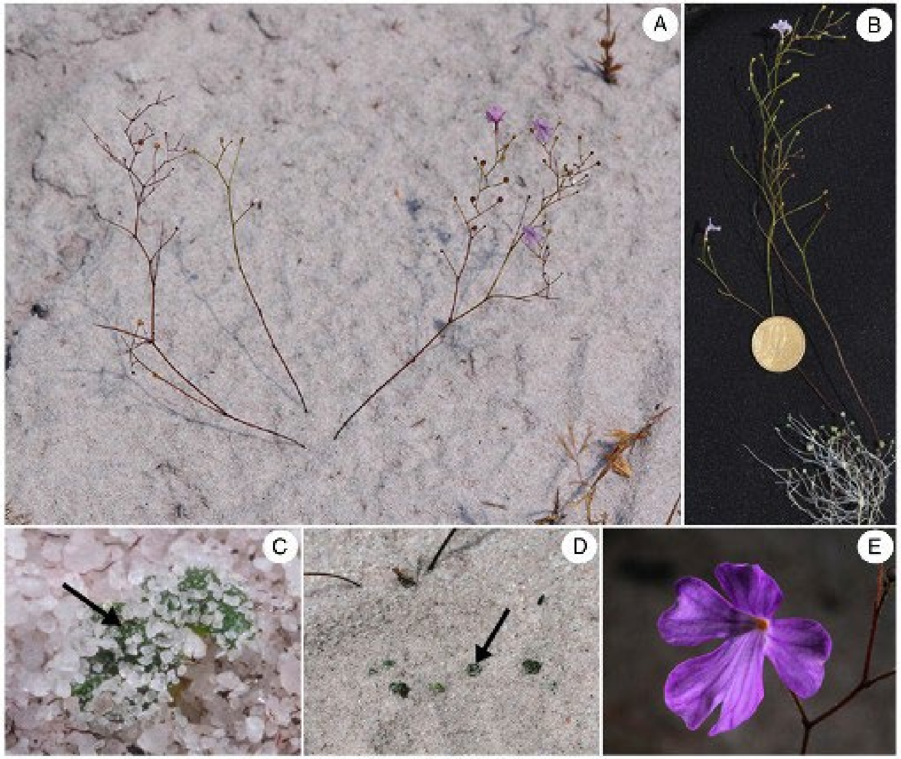
# The Plant of the D a y



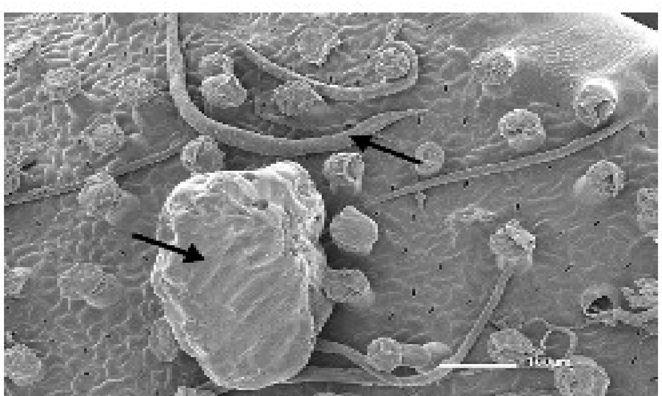

*Philcoxia*

Brazil

Well lit and low-nutrient habitat

Sticky underground leaves

Eats worms!



Pereira et al. 2012

# The evolution and maintenance of plant sexual diversity

# Questions

- What are plant mating systems?
- What are the major costs and benefits of selfing?
- What are the consequences of selfing on genetic variation and why?

# Mating Systems

Mating system: the mode of transmission of genes from one generation to the next through sexual reproduction (e.g. maternal selfing rate)

Selfing rate (*s*): the proportion of seeds that are self fertilized

Outcrossing rate (t=1-*s*): the proportion of seeds that are outcrossed

The outcrossing rate of a population can be estimated from genotyping seed families

# Sexual Systems

Sexual system: the particular deployment of sexual structures within and among plants and the physiological mechanisms governing mating

# Why do we care about the evolution of reproductive traits?

They influence their own transmission and the transmission of all other genes

Shift in mating system can strongly influence genetic variation, speciation and evolutionary diversification

It is just really cool

# The evolution of self-fertilization

14% of angiosperm species have evolved a predominantly selfing strategy

What is a major cost of self fertilization?
-inbreeding depression: the reduction in viability and fertility of inbred offspring compared with outbred offspring.
$\delta=1-w_s/w_o$

What causes inbreeding depression?
-homozygosity of recessive deleterious alleles
-loss of overdominance (heterozygote advantage)

# How would you assess inbreeding depression?

Greenhouse/field experiment

-Self and outcross plants
-Measure progeny fitness
-Calculate inbreeding depression
$\delta = 1 - w_s / w_o$

# How would you assess inbreeding depression?

Using genetic markers compare inbreeding coefficient of parents and progeny (Ritland 1990)

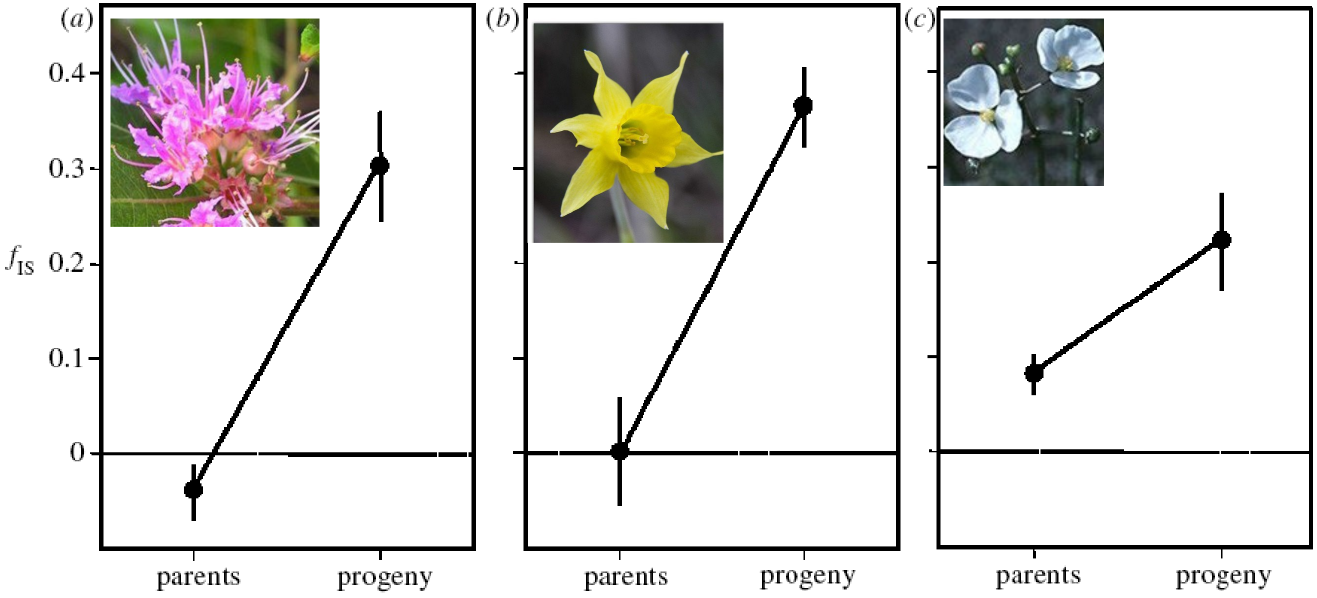



Figure 2. Selection against selfed progeny in populations of three animal-pollinated plant species with mixed mating systems. In each species there are significant changes in the mean inbreeding coefficient between parents and progeny estimated using allozyme markers. (*a*) Tristylous *Decodon verticillatus*: 10 populations, data in Eckert & Barrett (1994); (*b*) sexually monomorphic *Narcissus longispathus*: six populations, data in Barrett *et al.* (2003); and (*c*) monoecious *Sagittaria latifolia*: six populations, data in Dorken *et al.* (2002). Standard errors of the parental generation were estimated by bootstrapping data from Ritland's multilocus outcrossing rate program and those for progeny were the sum of the standard errors from estimates of selfing rates and parental $F$ (see Ritland 1990).

# Self fertilization

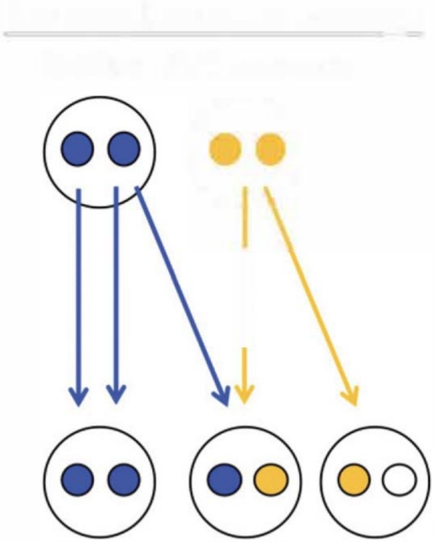
*Why do so many species self despite the cost of inbreeding depression?*

# Self fertilization

What is a major benefit of selfing?

i. Transmission advantage (Fisher)

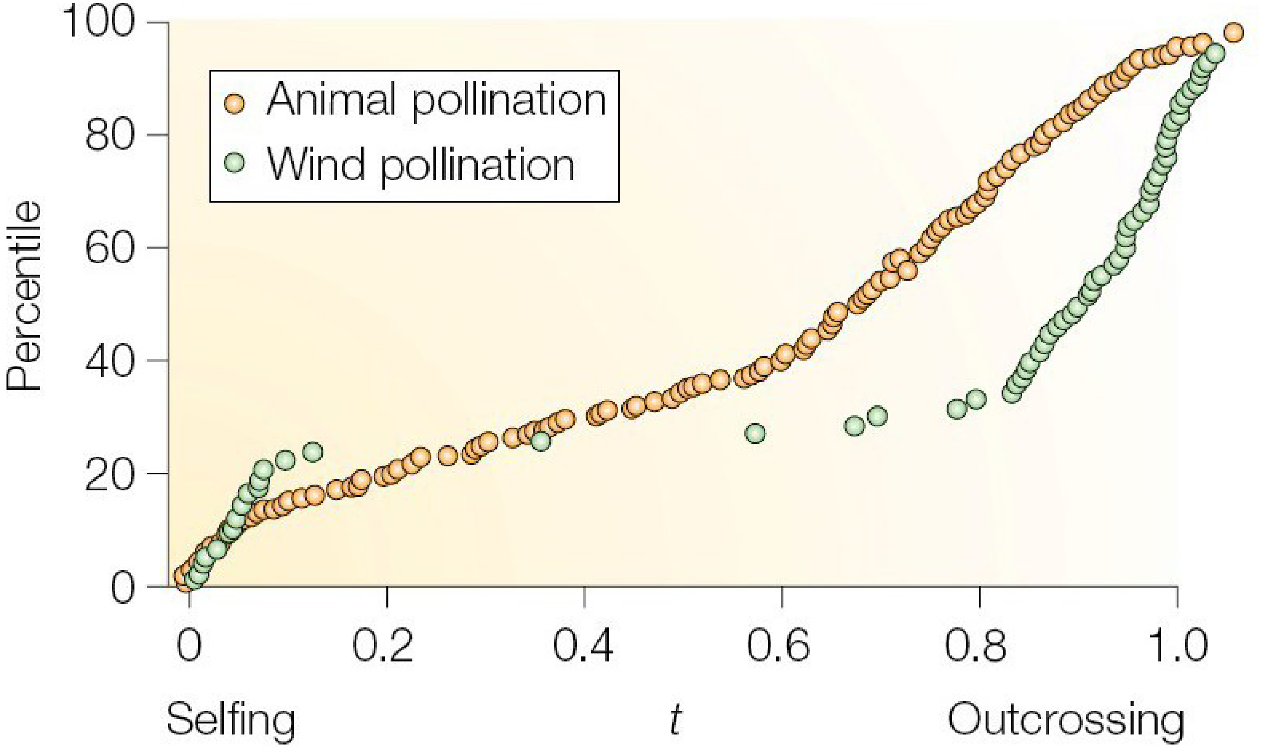
| | pollen parent | seed parent | total |
|---|---|---|---|
| outcrossing | 1 | 1 | 2 |
| selfing | (1 out+1self=2) | 1 | 3 |



The transmission advantage lost if $\delta > 0.5$

Early models on the evolution of selfing predicted that only fully outcrossing or selfing would be evolutionary stable strategies

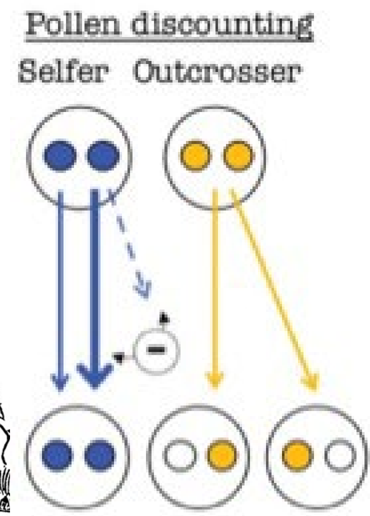
# The evolution of self-fertilization

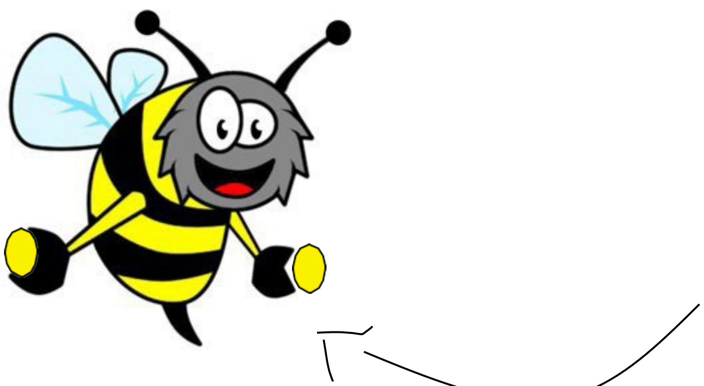


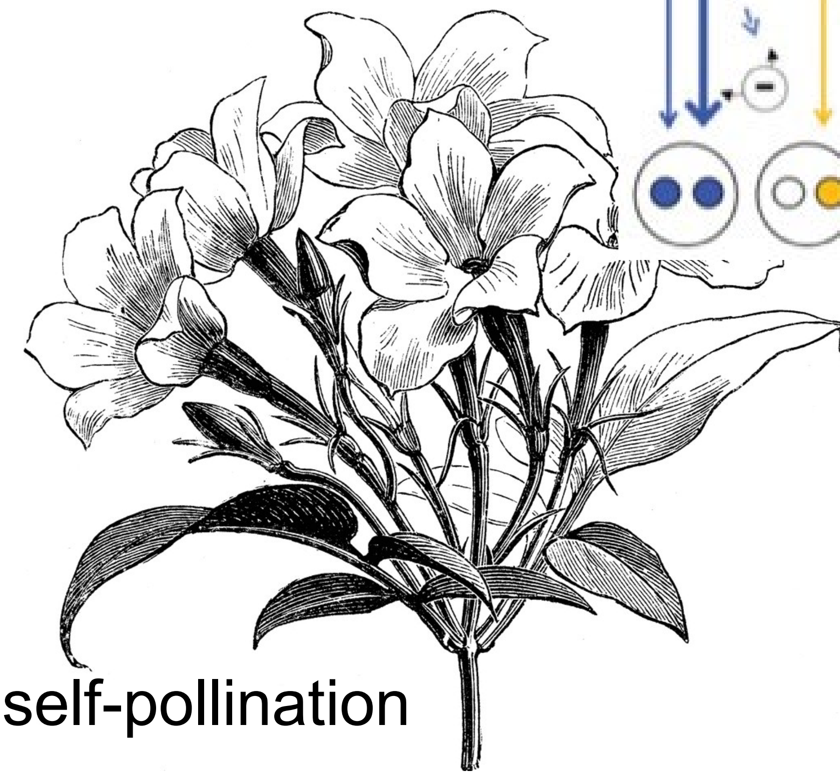

*Why do so many species have a mixed mating strategy?*

# Self fertilization: pollen discounting

Additional costs of selfing?
ii. pollen discounting: the loss in outcrossed siring success as a result of self-pollination





Geitonogamy: between flower self-pollination

# Self fertilization: pollen discounting

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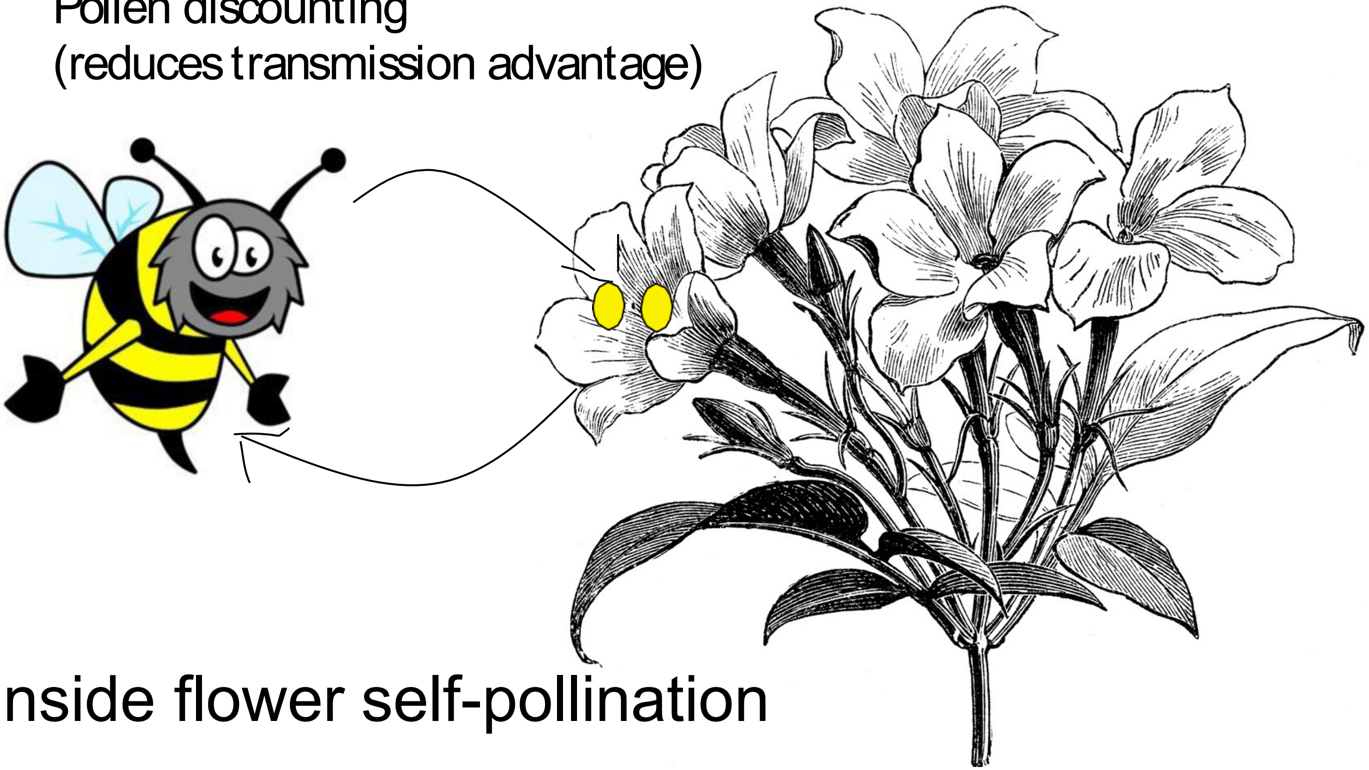
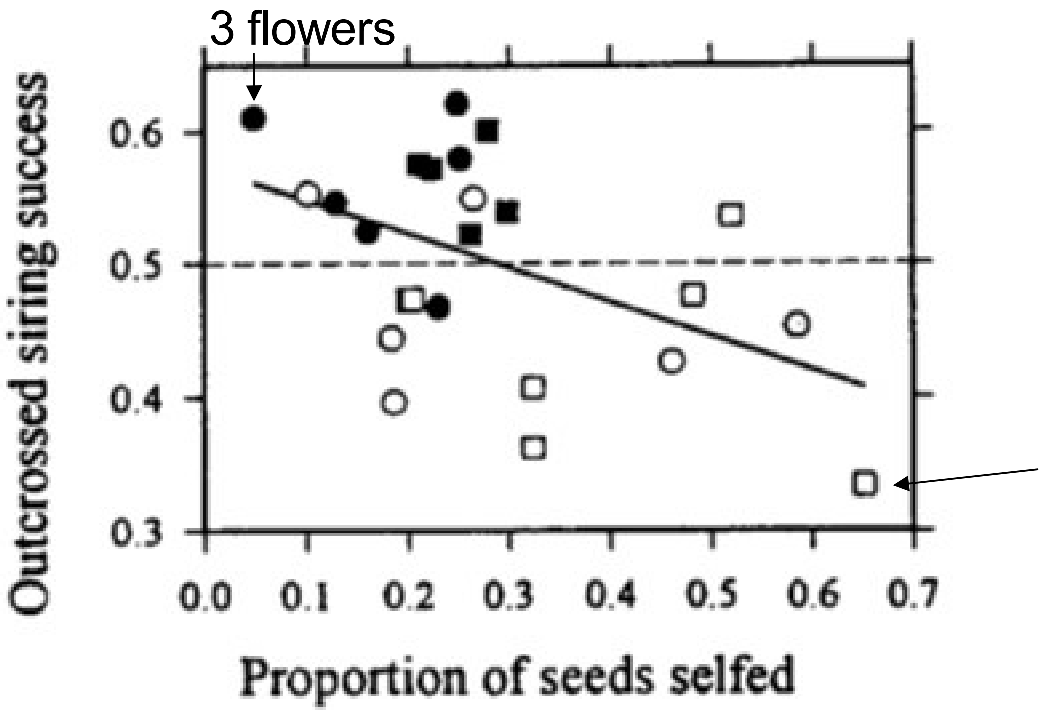



Autogamy: inside flower self-pollination

# Pollen discounting in *Eichhornia paniculata*

*Spencer Barrett*




Harder and Barrett 1995 Nature

Negative association between outcrossed siring success and selfing rate provides evidence for pollen discounting

The more flowers/inflorescence the more pollen discounting

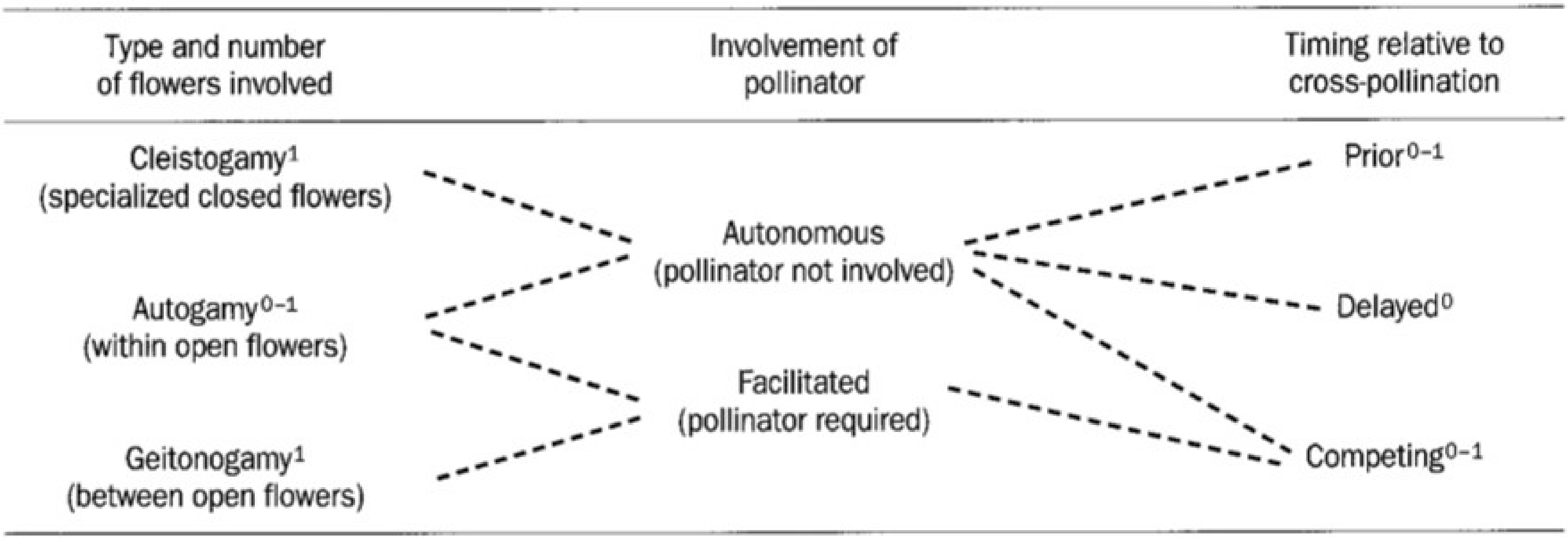
# Self fertilization

Additional benefits of selfing?

ii. Reproductive assurance: assured reproduction through selfing when conditions for outcrossing are not favourable (absence of mates or pollinators)


iii. Reduce gene flow and facilitate local adaptation (i.e., reduce outbreeding depression)

# Modes of self pollination




From Harder and Barrett 1996 TREE

Which type of selfing should be favored when there are few pollinators?

# Mating system is correlated with morphological and life history traits

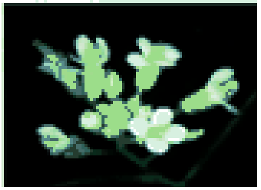
## What changes in floral morphology are correlated with selfing?

*Eichhornia paniculata*

*Amsinckia furcata* *A. vernicosa*


Arabidopsis lyrata - SI

Arabidopsis thaliana - SC



*Mimulus guttatus*

*M. nasutus*

**Selfing**

-Smaller flowers

-Less attractive

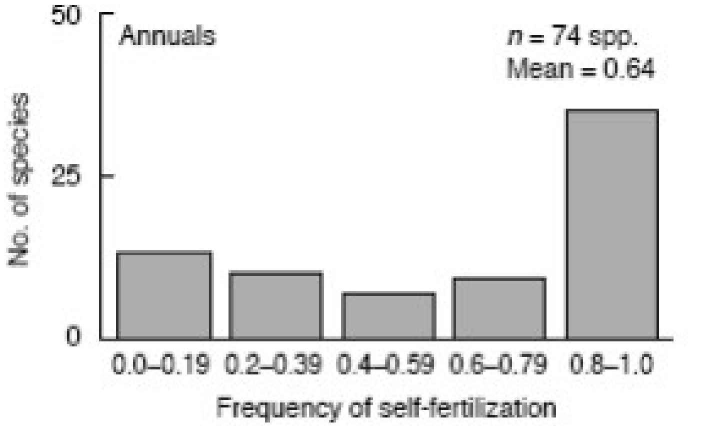
-Fewer rewards

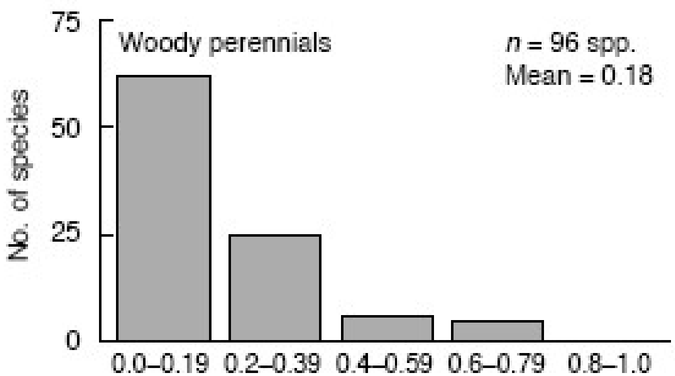
-Lower pollen production

-Smaller stigma-anther distance

# Mating system is correlated with morphological and life history traits

What life history traits are associated with the evolution of selfing?




Annuals tend to be selfers

Why?
Reproductive assurance

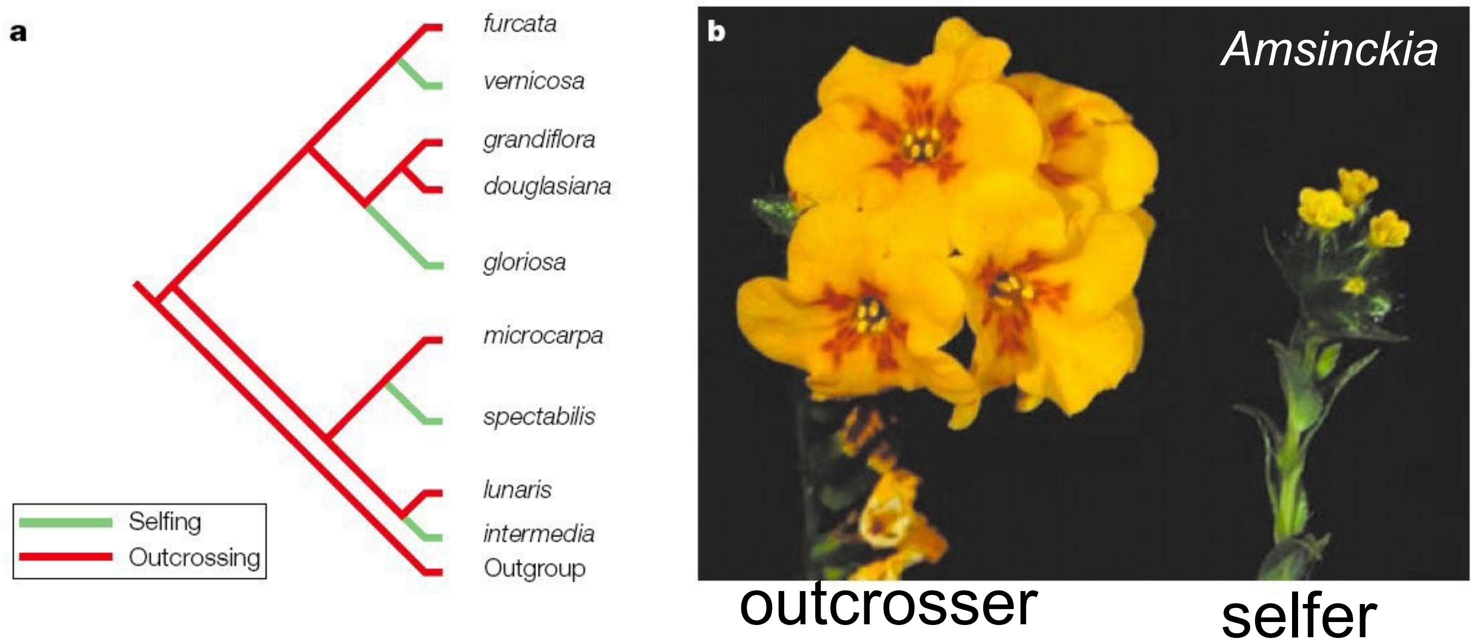
Perennials tend to be outcrossers

Why?

-costs to future survival and reproduction

Barrett et al 1996

# Evolutionary transitions from outcrossing to selfing

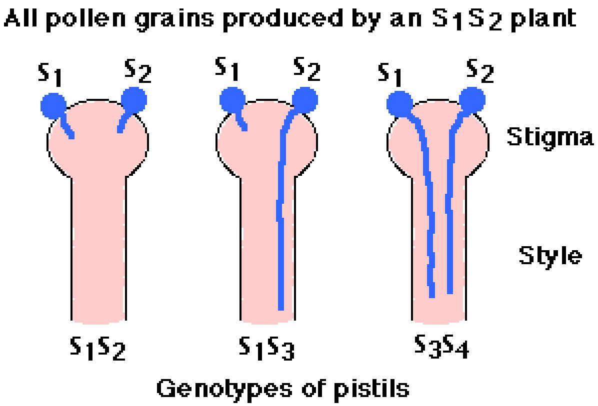



Multiple origins of self-fertilization

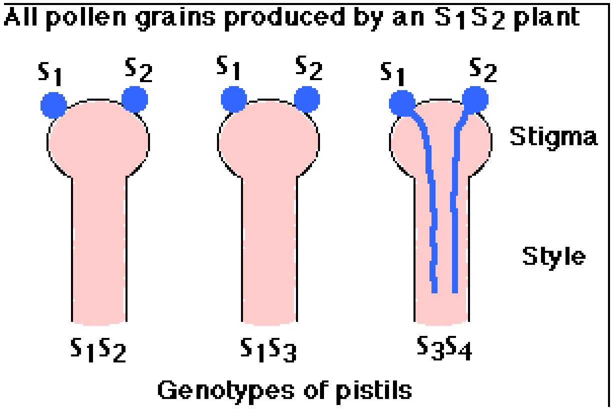
The evolution of selfing is thought to be a unidirectional shift
Why?

# Homomorphic self incompatibility

Two main types of homomorphic incompatibility (up to 50% of angiosperms)




-gametophytic: incompatibility phenotype is determined by its haploid genotype
e.g. S1 or S2 can not fertilize S1S2 plants but S3 pollen can




-sporophytic: incompatibility governed by the genotype of the pollen producing parent
e.g. any pollen from an S1S2 plant can not fertilize an SI_ or S2_ plant

# Homomorphic self incompatibility

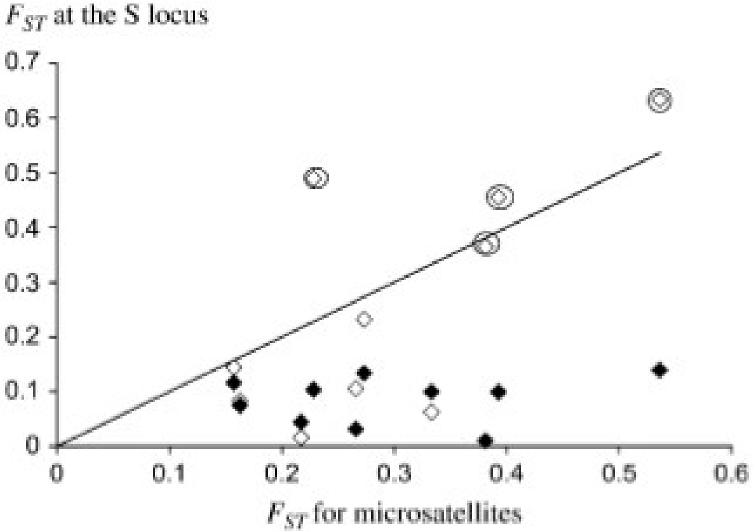
Maintained by negative frequency dependent selection (balancing selection):

Rare SI types have a fitness advantage as they can mate with all other plants in the population

Many S alleles

Low Fst compared to neutral loci (higher effective migration due to balancing selection)

*Brassica*




Glemin et al. 2005

# Is selfing a dead end? Long term costs and species selection

Goldberg et al. Science 2010

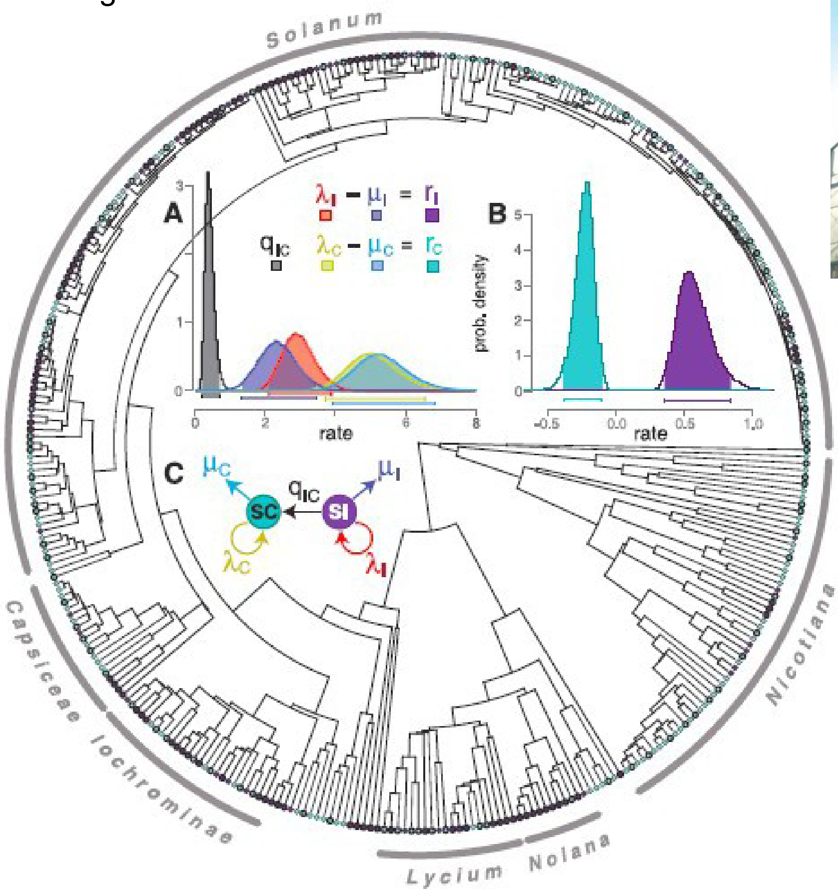



**Fig. 1.** Maximum likelihood tree of phylogenetic relationships among 356 species of Solanaceae. Higher ranks are indicated around the perimeter of the tree. Purple and turquoise tip colors denote SI and SC extant species, respectively. The root age is 36 million years. Inset panels display posterior probability distributions and 95% credibility intervals of reconstructed rates of character evolution (the time unit is millions of years). **(A)** BiSSE estimates of transition, speciation, and extinction parameters ($q_{IC} << \mu_I < \lambda_I << \lambda_C < \mu_C$). **(B)** Net diversification rate—the difference between speciation and extinction rates—associated with each state. **(C)** Schematic summary of estimated rate parameters. For methods, species names, character states, and further results, see (*19*).

Boris Igic

Emma Goldberg

*Solanum dulcamara*

SC species have high speciation rates but even higher extinction rates

SI species have lower speciation rates but even lower extinction rates

Long term costs to selfing?

# What are the consequences of selfing for genetic variation?

Selection and drift reduce genetic variation in inbred populations

**Selfing and drift**

-Completely selfing populations are expected to have a two-fold reduction in effective population size (*Ne*)
-Therefore drift is stronger in selfing vs outcrossing populations
-Reduces ability of selection to purge deleterious alleles or fix advantageous ones

**Selfing demography and drift**

-The capacity for uniparental reproduction gives selfers high colonizing ability
-Bottlenecks and lower census population size can further reduce *Ne* (thereby increasing drift)

# What are the consequences of selfing for genetic variation?

definitions

Selective sweep: an advantageous variant rises to fixation eliminating polymorphism at this locus

Genetic hitchhiking: when an allele increases in frequency because it is linked to a locus under positive selection

Background selection: negative selection reduces variation at linked neutral loci

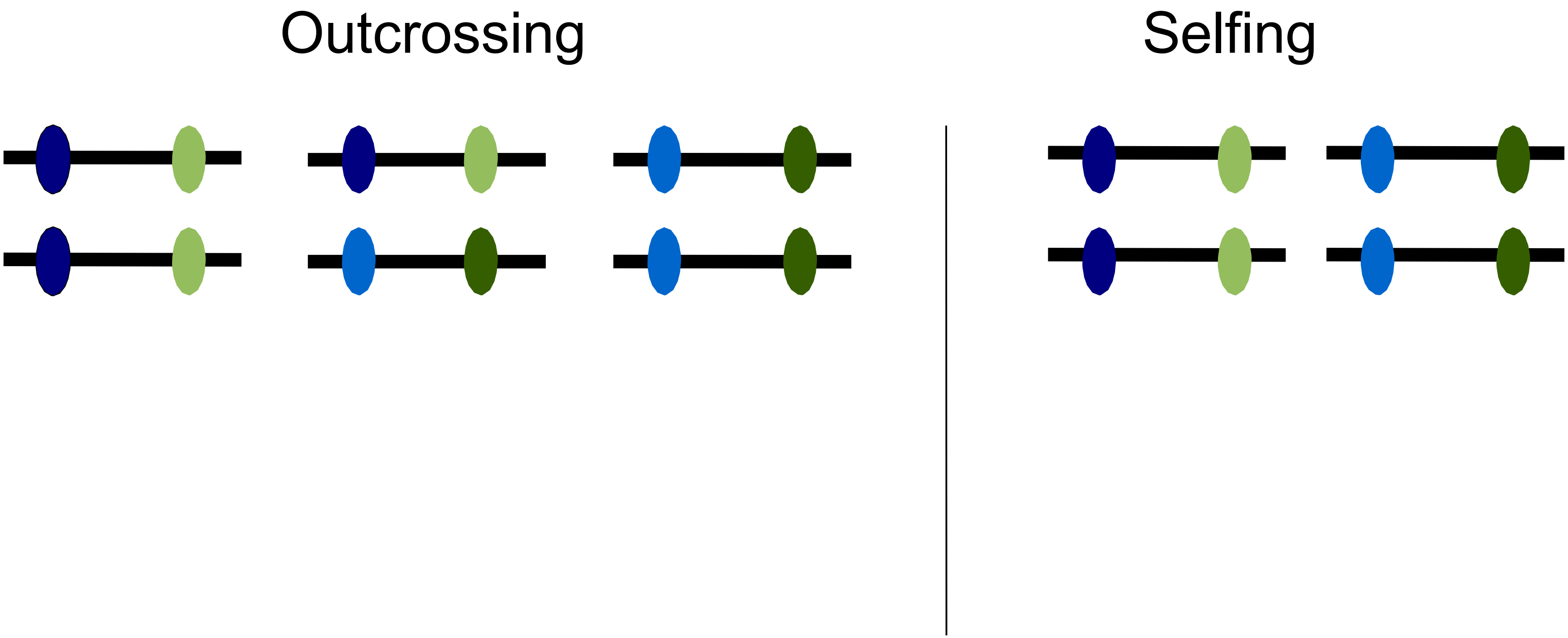
# What are the consequences of selfing for genetic variation?

**Selection**

-Reduced effective recombination in selfers (due to increased homozygosity)

# What are the consequences of selfing for genetic variation?

Reduced effective recombination

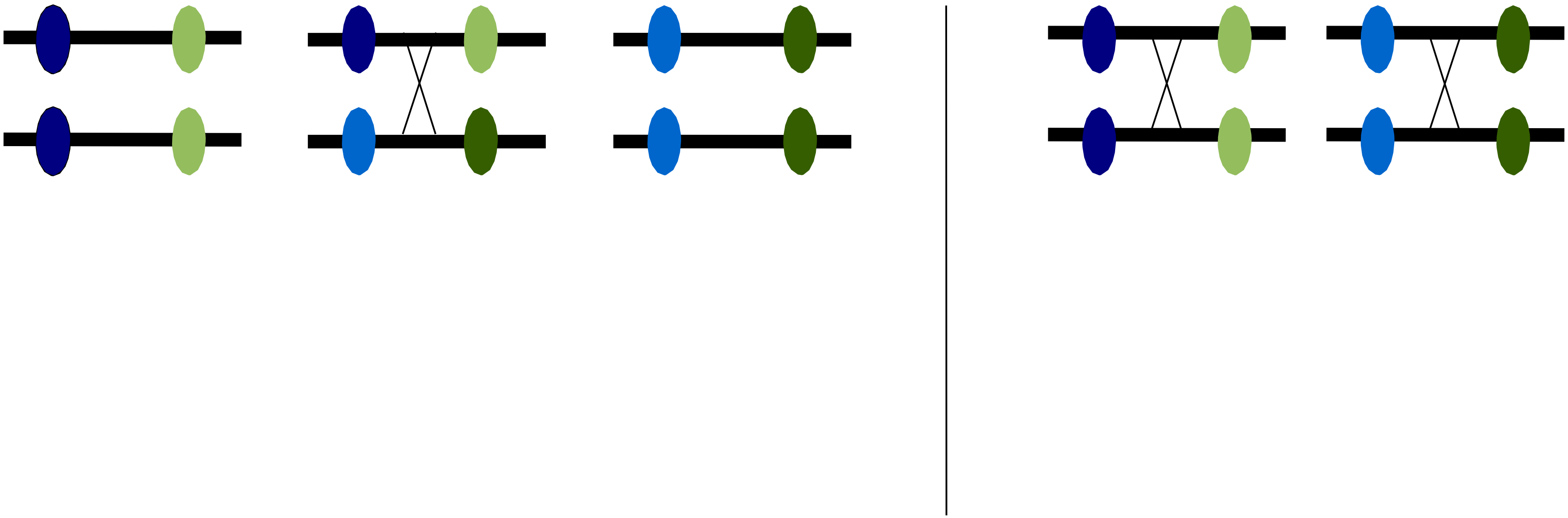



Wright et al. 2008

# What are the consequences of selfing for genetic variation?

Reduced effective recombination

Outcrossing Selfing



Wright et al. 2008

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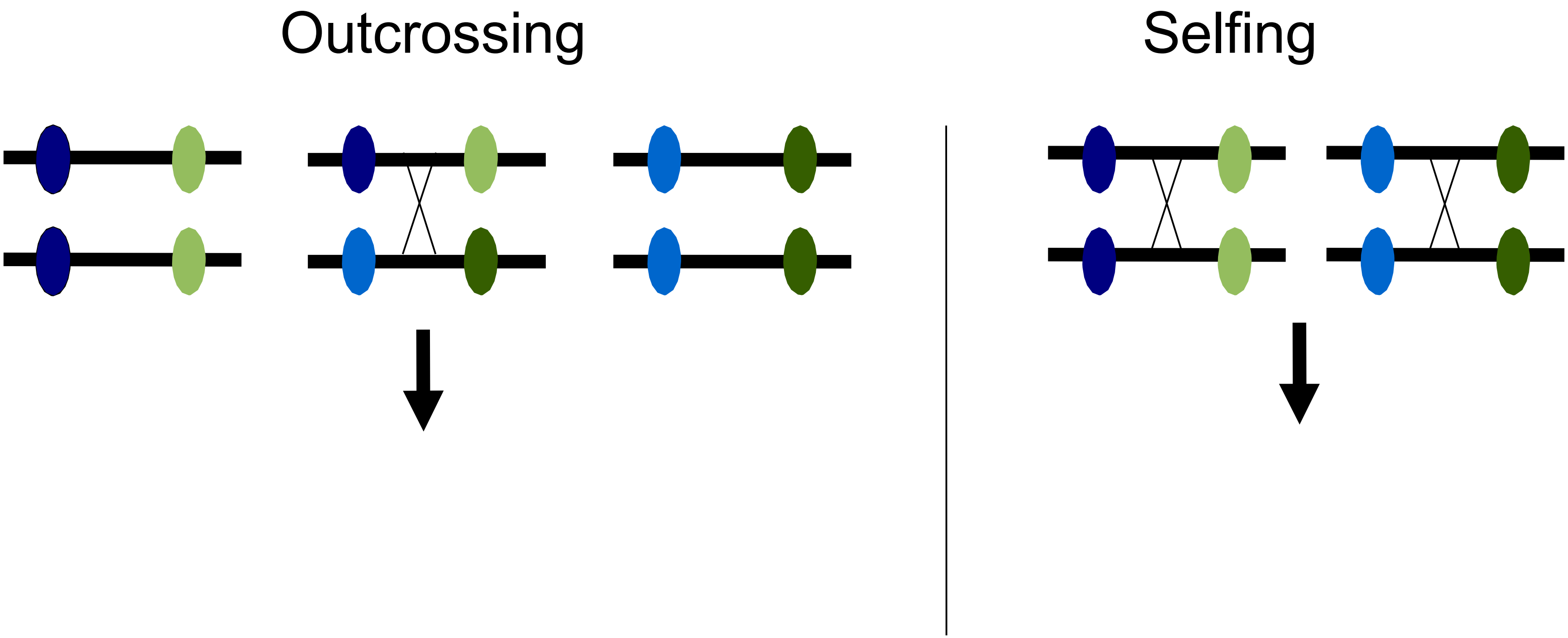


Wright et al. 2008

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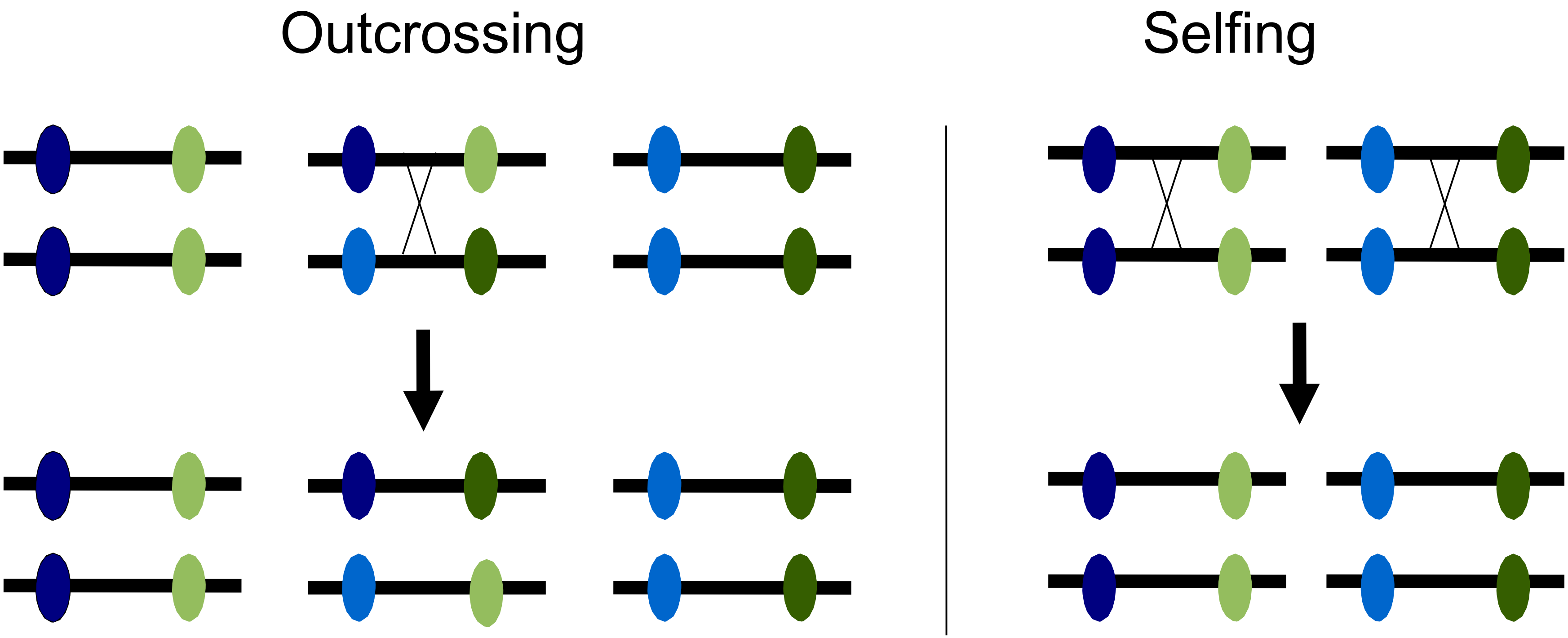



Wright et al. 2008

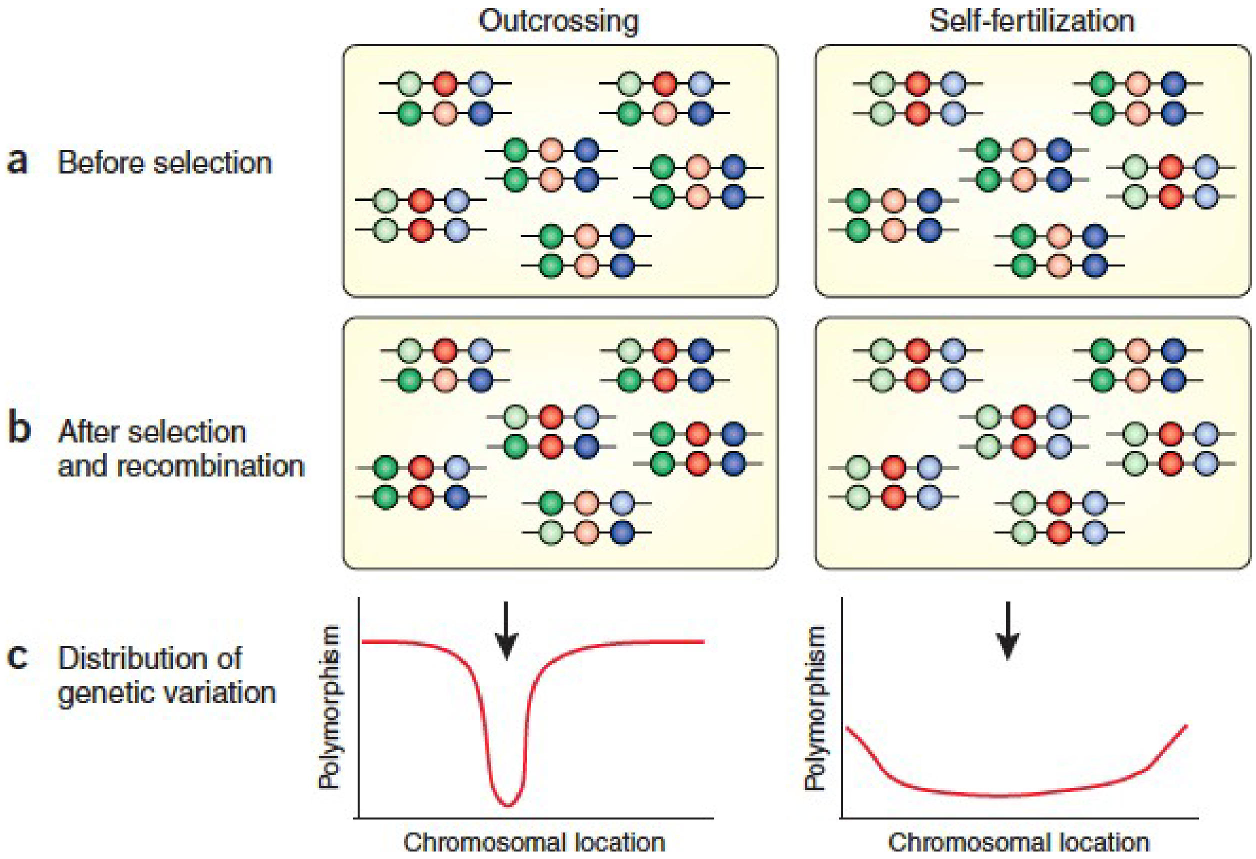
# What are the consequences of selfing for genetic variation?

**Selection**

-Reduced effective recombination in selfers (due to increased homozygosity)

-Positive selection (selective sweep) or selection against deleterious mutations (background selection) reduces variation at linked loci

# What are the consequences of selfing for genetic variation?




Influence of a self-fertilizing mating system on the patterns of genetic variation across the *Caenorhabditis elegans* genome (Phillips 2012).

# What are the consequences of selfing for genetic variation?

Does genetic variation in outcrossing and selfing taxa follow these predictions?

| Species | Genetic diversity (outcrossers vs selfers) |
|---|---|
| *Eichhornia paniculata* | 2x |
| *Solanum SI/ SC* | 4 to 40x |
| *Mimulus guttatus/nasutus* | 7x |
| *Arabidopsis lyrata/thaliana* | 4x |

# Mating system summary

Ecological and genetic factors influence the evolution of self fertilization from outcrossing

Selfing is associated with a number of morphological and life history traits

Mating systems and associated demographic traits have strong consequences for genetic variation, as well as speciation and extinction rates

Selfing can have many short term advantages, but appears to be an evolutionary dead end (high speciation rate and extinction rate)

# Unanswered questions

- What genetic changes are commonly associated with the transition to selfing?
- How have transitions away from selfing ocurred?
- How will selfing rates affect adaptation to a changing climate?